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SHORT COMMUNICATION

The bigger the better? Vigour of the exotic host plant *Calotropis procera* (Apocynaceae) affects herbivory

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Abstract

The Plant Vigour Hypothesis states that herbivores preferentially feed on the most vigorous plants within a plant population and/or the most vigorous modules within a plant. The goal of this study was to evaluate how shoot size (as an indication of module vigour) affects leaf herbivory in the host plant *Calotropis procera*, an exotic xerophyte perennial milkweed shrub. We predicted that the proportion of leaf area removed by insect herbivores would be positively related to shoot size. Eight patches were selected containing a varied number of *C. procera* individuals (5, 8, 29, 31, 55, 79, 116, and 172 individuals/patch) in the Brazilian seasonally dry vegetation (Caatinga), of which five individuals were randomly selected for further analysis. From each individual, three to six shoots were randomly selected, measured and had their leaves collected, for a total of approximately 200 leaves per patch. At the regional scale, the proportion of leaf area removed was positively affected by shoot size. In addition, this pattern was also found for the majority of the studied patches (29, 31, 55, 116, and 172 individuals/

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patch). Among the insect herbivores associated with *C. procera*, larvae of *Danaus* spp. (Lepidoptera: Nymphalidae) were commonly observed feeding on all patches. These herbivores present a specialized behaviour to circumvent the presence of latex in the host leaves. Although more vigorous plant modules should be better defended compared with the less vigorous modules, *Danaus* species were able to bypass host defences, and feed on healthy, rapidly growing and vigorous plant modules of *C. procera*, hence causing more damage to these modules.

Keywords
Caatinga, *Danaus*, insect-plant interactions, invasive species, Plant Vigour Hypothesis

Introduction

The choice of plant hosts by adult insect herbivores and the subsequent development and performance of their offspring is a central issue to understand the evolution of plant-herbivore interactions (Thompson 1988). Ovipositing females should select the quality of the hosts on which larval performance would be greatest to maximize their own fitness, since young instars of herbivorous insects have little or no capacity to move after parental oviposition (Jaenike 1978; Santos et al. 2008; Gripenberg et al. 2010; Griese et al. 2020). Plant quality parameters, such as size, nutritional quality, and defences, have been consistently used to explain the preferences of insect herbivores by certain hosts or organs and consequently their larval performance (De Bruyn et al. 2002; Price and Gerling 2004; Heisswolf et al. 2005; Santos et al. 2008; Han et al. 2014; Salgado and Saastamoinen 2019).

In this context, the Plant Vigour Hypothesis proposed by Price (1991) states that herbivores prefer to feed on most vigorous plants within a plant population and/or the most vigorous modules within a plant. The term 'vigour' means any plant in a plant population or any module, such as a shoot or leaf, that grows rapidly and ultimately reaches a large size, relative to the mean growth rate and ultimate size achieved in the population of plants or population of modules (Price 1991). An increase in food resources, oviposition sites and nutritional quality are among the mechanisms used to explain the positive relationship between the preference/abundance of insect herbivores with the vigour of host plants (Price et al. 1990; Price and Gerling 2004; Heisswolf et al. 2005; Han et al. 2014). A meta-analysis found a consistent pattern of strong and positive effects of plant vigour on the abundance of different herbivore feeding guilds, such as sap-suckers, leaf-miners, gall-inducers, and chewers (Cornelissen et al. 2008).

Calotropis procera (Aiton) WT Aiton (Apocynaceae) is a xerophyte perennial milkweed shrub native to Asia and Africa, which has been widely introduced into many parts of the world (Hassan et al. 2015). In Brazil, this invasive plant species is widely distributed in the northeastern region, into the Cerrado and Caatinga biome domains (Ulhôa et al. 2007; Rangel and Nascimento 2011). Plant characteristics such as anemochory and easy propagation have allowed the formation of large populations mainly in disturbed areas, such as in pastures and roadsides (Ulhôa et

al. 2007; Fabricante et al. 2013). In addition, *C. procera* presents fast growth, with several shoots sprouting from a single individual, and vigorous and green leaves are present throughout the year. These large leaves may represent an important resource for insect herbivores, especially in strongly seasonal environments such as the semi-arid Brazilian Caatinga (Fernandes et al. 2020). Despite the fact that this species is very well defended against attack by insect herbivores, especially with latex and toxic steroidal cardenolides (Agrawal et al. 2012), many species from Coleoptera, Hemiptera and Lepidoptera orders have been reported consuming *C. procera* leaves (Chandra et al. 2011; Dhafer et al. 2012).

The goal of this study was to evaluate how shoot size (as an indication of module vigour) affects leaf herbivory in the exotic host plant *C. procera*. More specifically, we used the higher variety of shoot sizes sprouting from *C. procera* individuals to test the Plant Vigour Hypothesis (Price 1991), and predicted that the proportion of leaf area removed by insect herbivores would be positively related with shoot size.

Methods

Study area and sampling design

The study was carried out between March and April 2006 in an area belonging to the Agronomic Institute of Pernambuco, located in the municipality of Serra Talhada, Pernambuco, Brazil. The climate of the region is seasonal with an average annual precipitation of approximately 800 mm, concentrated from January to May, and the annual average temperature of 26 °C (Sampaio 1995). The local biome is Caatinga, xeric shrubland dominated by an arboreal-shrubby physiognomy (Ferraz et al. 1998). The herbaceous stratum is not very dense and is mainly composed of annual plants that grow only in the rainy season (Sampaio 1995).

To evaluate the effect of shoot size on insect herbivory eight patches were selected containing a varied number of *C. procera* individuals (5, 8, 29, 31, 55, 79, 116, and 172 individuals / patch). In order to estimate leaf herbivory in the patches, all plants higher than one meter and with more than ten shoots were pre-selected. Of these, five were randomly selected in each patch. From each individual, three to six shoots (young shoots produced in the current season) were randomly selected, from which their leaves were collected, for a total of approximately 200 leaves per patch. The leaf area removed was calculated by dividing the sum of all areas removed from a leaf by the total area of the respective leaf. The leaf images were analyzed using the Image Tool 1.1 program. The proportion of leaf area removed on each plant individual was determined by averaging the leaf area removed from each shoot per individual.

Statistical analysis

A Generalized Linear Model (GLM) with a "*Quasi-binomial*" distribution of errors was used to test whether the proportion of leaf area removed by insect herbivores

is positively affected by shoot size of *C. procera* individuals. The proportion of leaf area removed was used as the response variable, shoot size and its interaction with patch identity were used as explanatory variables. Thus, the effects of shoot size on the proportion of the leaf area removed were first tested in a regional context and, later, specifically for each patch. A p-value less than 0.05 (< 0.05) was considered statistically significant. The statistical analysis was conducted with the R software (R Core Team 2020).

Results and discussion

At the regional scale, the proportion of the leaf area removed was positively affected by shoot size ($R^2 = 0.29$; $p < 0.001$; Fig. 1). However, this response varied between patches ($p < 0.001$). No significant relationship was found between shoot size and herbivory in the patches with 5 and 8 *C. procera* individuals ($p = 0.88$ and $p = 0.06$, respectively). However, we found a negative relationship between shoot size and the proportion of the leaf area removed in the patch with 79 *C. procera* individuals ($F = 6.25$; $R^2 = 0.18$; $p = 0.018$; Fig. 2A), while a positive relationship was found for patches containing 29 ($F = 84.25$; $R^2 = 0.75$; $p < 0.001$; Fig. 2B), 31 ($F = 64.4$; $R^2 = 0.76$; $p < 0.001$; Fig. 2C), 55 ($F = 104.84$; $R^2 = 0.84$; $p < 0.001$; Fig. 2D), 116 ($F = 187.79$; $R^2 = 0.81$; $p < 0.001$; Fig. 2E), and 172 *C. procera* individuals ($F = 473.23$; $R^2 = 0.91$; $p < 0.001$; Fig. 2F).

Despite the fact that no quantitative data on the abundance of the insect herbivore species associated with *C. procera* was collected in this study, larvae

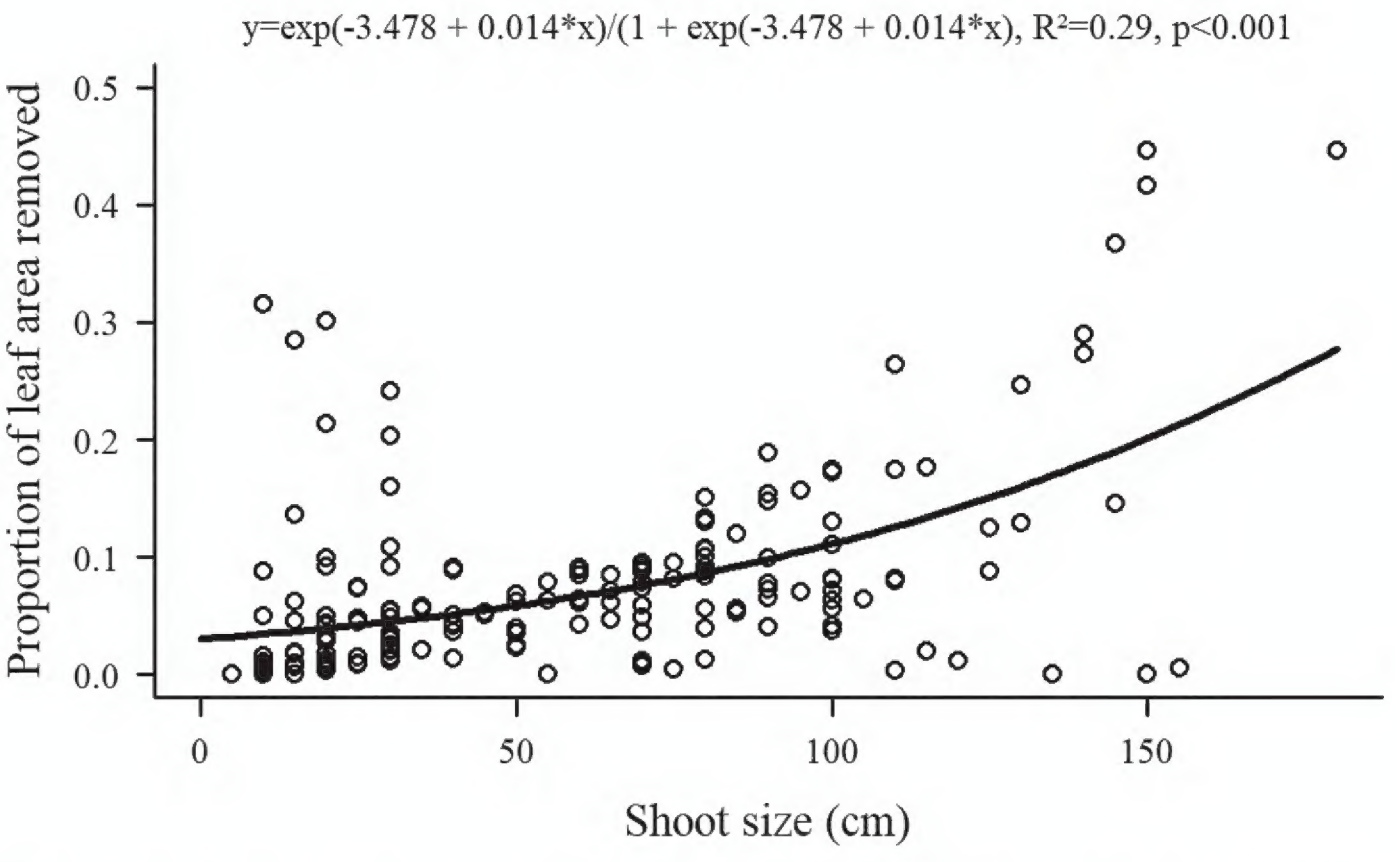

Figure 1. Relationship between the proportion of the leaf area removed by insect herbivores and shoot size of *C. procera* individuals in the Caatinga, Pernambuco, Brazil.

of *Danaus* spp. (Lepidoptera: Nymphalidae) were commonly observed feeding on all patches (Fernandes et al. 2020). In fact, larvae of the three *Danaus* species that occur in the Brazilian Caatinga, *D. erippus*, *D. gilippus* and *D. eresimus*, were observed feeding on *C. procera*, while chewing insects from other orders, such as Coleoptera and Orthoptera, were observed feeding on a few individuals ($n < 10$; M.F.V. Rodrigues-Menelau *personal observation*).

At a regional scale, the present study supports the Plant Vigour Hypothesis (Price 1991), because larger shoots of *Calotropis procera* had a greater proportion of leaf area removed by insect herbivores. This pattern was also recorded for the majority of patches, although an opposite pattern was observed for one of the eight studied patches. Our results also suggest that differences between patches, such as patch size, may have influenced some different responses found at patch scale, since both patches with fewer individuals (5 and 8) did not present any relationship between the proportions of leaf area removed and shoot size.

Although more vigorous plants should be better defended compared with less vigorous plants, specialist herbivores are expected to be more greatly affected by host-plant nutritional quality than plant defences because they have supposedly evolved adaptations to overcome plant defences (Price 1991). In this study, *C. procera* individuals were mostly attacked by *Danaus* butterflies, of which early instars present specialized behaviours to circumvent the presence of latex by performing trenching or vein-cutting on the leaf, and feeding only after the latex has drained, while late instars, which have already acquired greater resistance to latex, feed on the leaf margins (Rodrigues et al. 2010; Ferreira and Rodrigues 2015). These adaptations may have allowed *Danaus* species to prefer healthy, rapidly growing and vigorous plant modules of *C. procera* individuals and, consequently, causing more damage to these plant modules. In addition, adult females of *Danaus* spp. are probably more attracted to larger shoots due to the greater availability of oviposition sites and food resources for their larvae, thus avoiding intra-specific competition in smaller shoots. Otherwise, only future observation and experimental studies could shed light on this hypothesis.

Positive relationships between plant vigour and oviposition preference, abundance and larval performance for other species of lepidopterans have been widely reported (e.g., Freitas et al. 1999; Cunningham and Floyd 2006; Han et al. 2014; Griese et al. 2020). For example, Price and Gerling (2004) found that only vigorously growing shoots of *Tamarix nilotica* were attacked by the spindle-gall moth *Amblypalpis olivierella*, and that longer active shoots with more resource available supported more larvae and galls. Similarly, lepidopteran immatures of a tropical forest in Southeastern Brazil showed a clear pattern of occupation on younger leaves that are larger and on hosts with larger leaves than those not occupied (Freitas et al. 1999). Finally, Han et al. (2014) found that the Neotropical leafminer moth *Tuta absoluta* survived better and developed faster on the tomato plants with larger plant growth rate.

We conclude that the vigour of the exotic host plant *C. procera* is a major factor affecting insect herbivory. Our observations suggest that *Danaus* butterflies are the

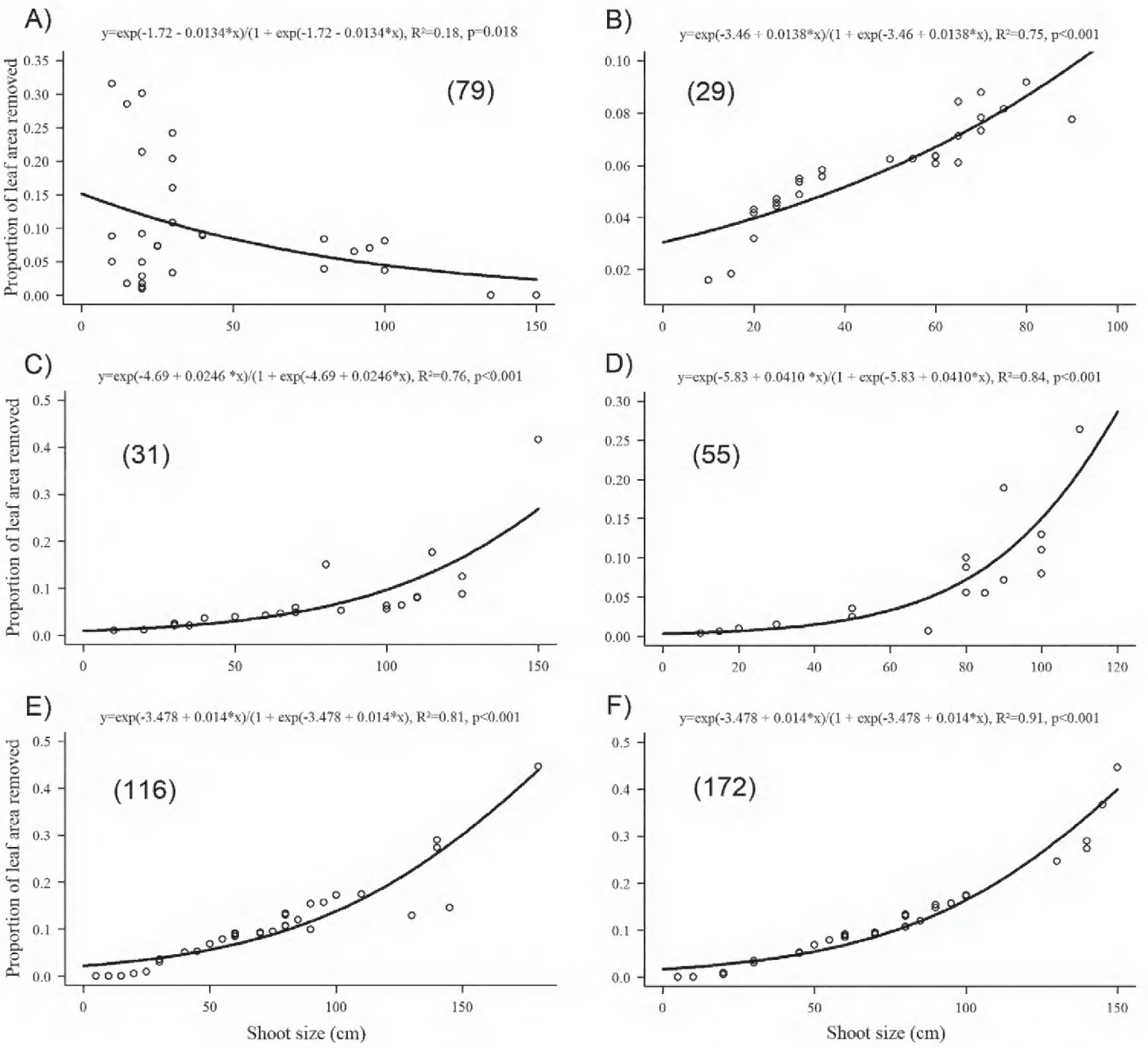

Figure 2. Relationship between the proportion of the leaf area removed by insect herbivores and shoot size of *C. procera* individuals in patches with 79 (**A**), 29 (**B**), 31 (**C**), 55 (**D**), 116 (**E**) and 172 (**F**) individuals in the Caatinga, Pernambuco, Brazil. The numbers in parentheses represent the number of individuals in the respective patch.

main insect herbivores feeding on *C. procera* in the study region. We highlighted that further studies are needed to investigate how the trends found in this study can vary between *Danaus* species in the Brazilian Caatinga, and whether larval performance of *Danaus* species is also increased in more vigorous modules of *C. procera*.

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